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STUDIES IN FOREST PATHOLOGY

XVIII

The Occurrence of the Indian Paint Fungus, *Echinodontium tinctorium* E. & E., in British Columbia

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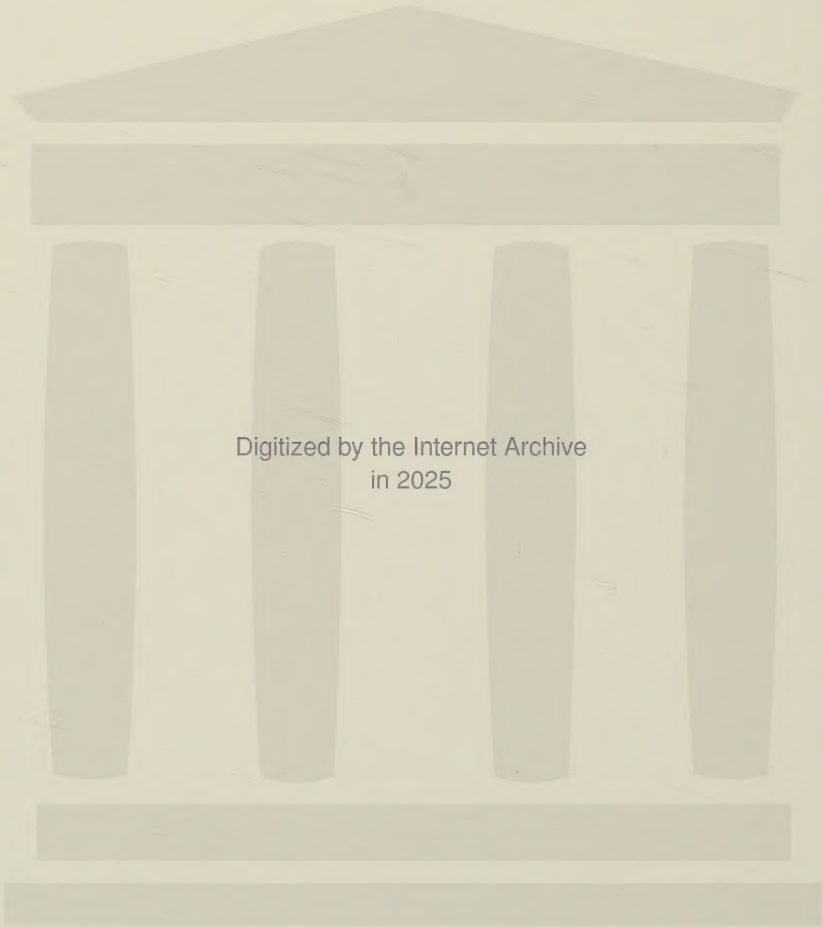

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INTRODUCTION

Echinodontium tinctorium E. and E., commonly called the Indian paint fungus, is constantly associated with a heartwood decay in certain coniferous trees of British Columbia. The destructive nature of this rot and the occasional high frequency of occurrence of the fungus has established it as one of the most important fungi that infect British Columbia conifers.

The original surveys made to determine its geographic distribution and appraise the damage resulting from it, showed that this fungus occurred throughout the ranges of its hosts and that uniformly serious losses from its associated decay could be expected in mature stands.

Later surveys, however, showed that extensive areas within the natural ranges of hosts of *E. tinctorium* were free of the fungus. Consequently, a concept of regional importance was ascribed to the fungus; *E. tinctorium* was considered to be absent from the Coast Mountains, to have a limited occurrence within the Cascade Mountains, and to be uniformly abundant in the interior "wet-belt" and sub-alpine forests.

However, a recent appraisal of the occurrence of *E. tinctorium* in British Columbia has demonstrated that the fungus varies in frequency in its regions of presumed high and low abundance (29). Similarly, an investigation of western hemlock, *Tsuga heterophylla* (Raf.) Sarg., in the upper Columbia region of British Columbia (13) showed a relationship between rot associated with *E. tinctorium* and the site quality of individual stands. The variations encountered within the region mentioned and the Province as a whole have been so great as to render untenable a strict concept of regional importance for the fungus. It became evident that a reappraisal of the distribution pattern of *E. tinctorium* was needed.

Because of its demonstrated importance *E. tinctorium* has been under investigation by the Forest Biology Laboratory, Victoria, British Columbia, since 1952. An investigation of the ecology of this fungus is continuing but the results to date permit reporting upon the progress made to reach the immediate objective, which is to provide a method for recognizing the forest conditions that favor its abundance.

LITERATURE REVIEW

The Indian paint fungus, was first described by Ellis and Everhart (11) as *Fomes tinctorius* and finally as *Echinodontium tinctorium* by Ellis (17). Most investigators believe that the fungus belongs to the *Hydnaceae* but some, like Miller (21), place it in the *Polyporaceae*. The final disposition of the fungus in the systematic arrangement of fungi remains undecided but certain features of *Echinodontium tinctorium* are already well known. The fungus produces a typical sporophore[3] in a characteristic manner beneath branch stubs of living trees and is associated with a distinctive heartwood decay in its development.

The sporophore (Figs. 1-6) is perennial in that it can remain active for several years by adding a fresh hymenium each year. But eventually it will cease to

[3] The term *sporophore* used herein is synonymous with the terms *hymenophore* and *fruit body*. It is not used to denote the true sporophore, which is a typical basidium.

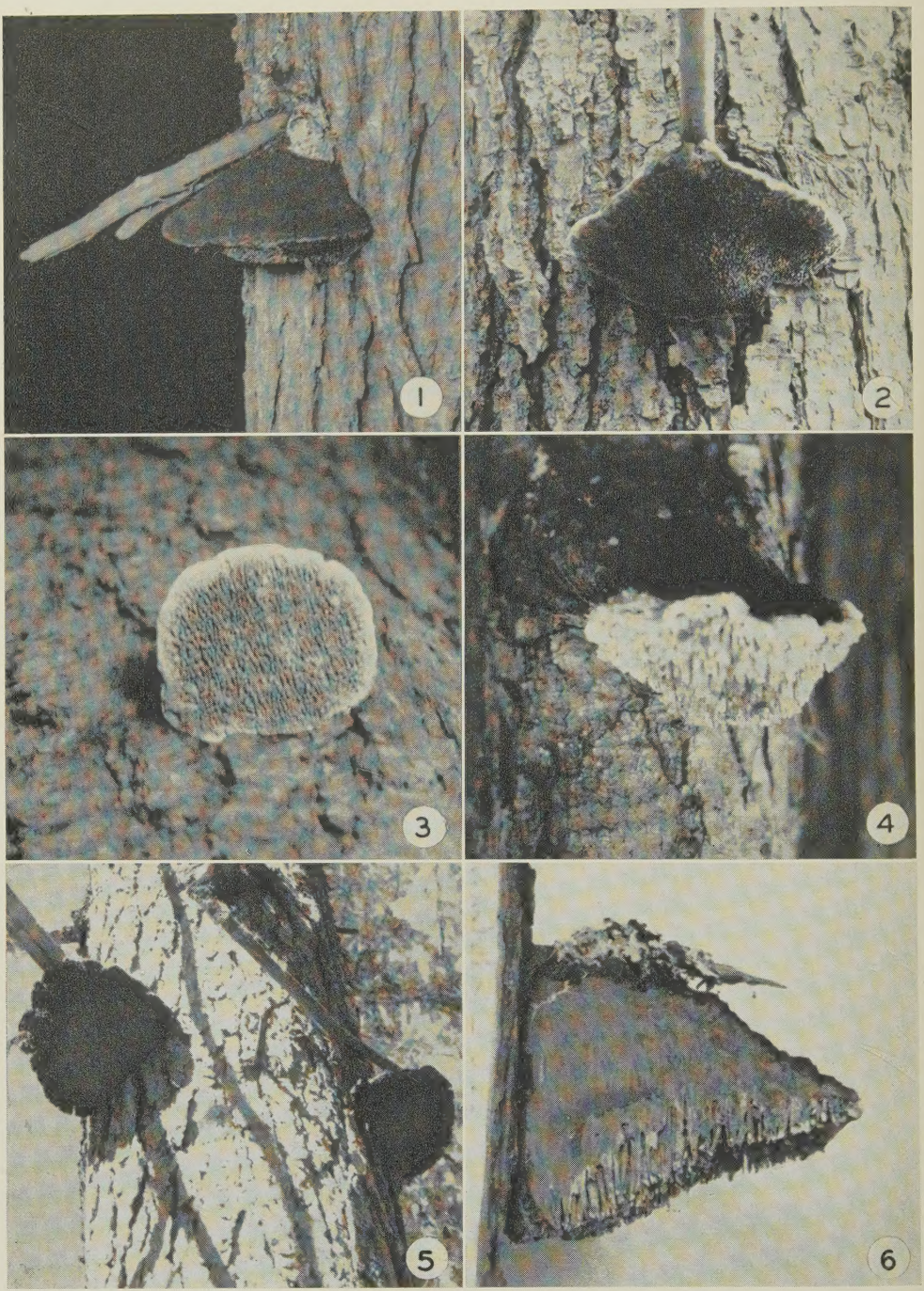

PLATE I

function as the size of its fruiting surface gradually shrinks (Fig. 5). The spores are produced on basidia in a hymenium that extends over the surfaces of the spines that cover the lower side of the sporophore; two or more crops are formed in early and late summer (16). The spores are airborne to potential courts of infection.

If germination and inoculation occur, the fungus develops an intra-cellular mycelium (15, 20) in the heartwood of living trees and eventually produces the typical associated rot. The sequence of decay development, although not fully known for all species of host, has been studied in detail by Mayers (20) for alpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and by Hubert (15) for western hemlock. Both of these investigators stressed the role of wood rays in decay development; they observed concentrations of hyphae of *E. tinctorium* in ray cells and a scarcity of them in surrounding tracheids.

The resultant decay (Figs. 7-12) is distinct from those caused by other fungi, except that in some of its advanced stages it closely resembles equivalent stages of rot associated with *Stereum sanguinolentum* Alb. & Schw. ex Fr. (2). Incipient rot is difficult to detect unless it is accompanied by either brown discolorations or red or brown streaks. Such rot may extend for several feet beyond visible rot (15). Wood in later stages of decay has a spongy texture and is yellowish with intermittent golden brown areas that later intensify to the characteristic reddish-brown color of final decay. Wood in the typical decay stage may be streaked with dark to red colors, sometimes has narrow dark zone lines, and is stringy and often laminate. Eventually the heartwood of infected trees is entirely disorganized and gives place to large cavities.

E. tinctorium was first reported from Alaska on hemlock and from Idaho on grand fir (*Abies grandis* (Dougl.) Lindl.) (17). After these early reports, Hedgcock (14) reported it on western hemlock, amabilis fir (*A. amabilis* (Dougl.) Forb.), corkbark fir (*A. arizonica* Merr.), white fir (*A. concolor* Lindl. & Gord.), alpine fir (*A. lasiocarpa* (Hook.) Nutt.), red fir (*A. magnifica* A. Murr.), noble fir (*A. nobilis* Lindl.), Engelmann spruce (*Picea engelmannii* Parry), and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco, all in the western United States. Weir and Hubert (28) reported it on mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and bristlecone fir (*Abies venusta* (Dougl.) Koch) and Tannhauser (26) isolated the fungus from western white spruce (*Picea glauca* (Moench) Voss var. *albertiana* (S. Brown) Sarg.), but was unable to locate its fruit bodies on this species.These reports indicate that western North American species of *Chamaecyparis, Juniperus, Larix, Pinus, Taxus, Thuja,* as well as Sitka spruce

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PLATE I

The gross features and habit of sporophores of *E. tinctorium*.

FIG. 1. The upper surface of older sporophores is black, hard, and fissured.

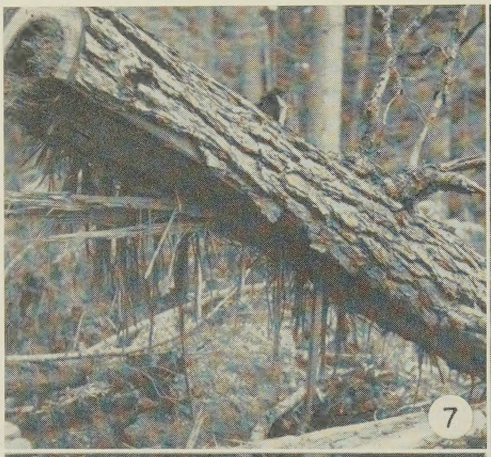
FIG. 2. The region of attachment of most sporophores is usually beneath branch stubs but occasionally on the lower side of living branches.

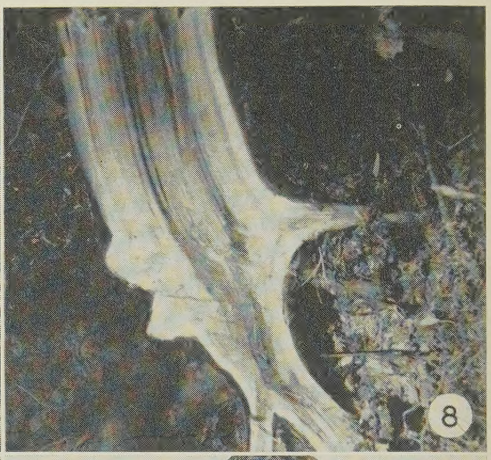
FIG. 3. The lower surface of young sporophores is typically daedaloid and is white to light brown in color.

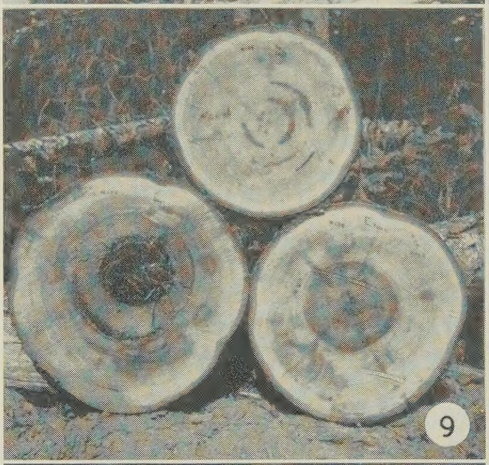
FIG. 4. The lower surface is creamy white when sporulation occurs.

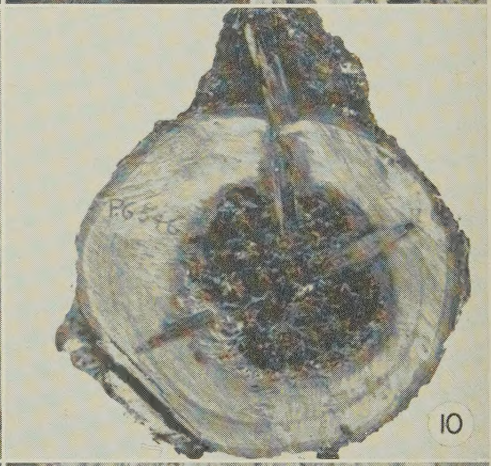
FIG. 5. An annual reduction in the extent of the functional portion of the lower surface occurs in older sporophores.

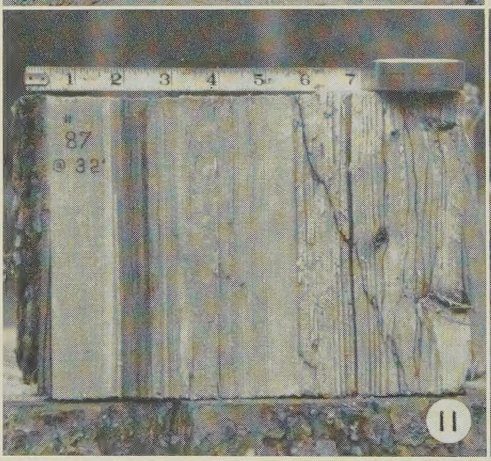
FIG. 6. The hymenium is arranged over the surface of the spines that project downward from a brick red context.











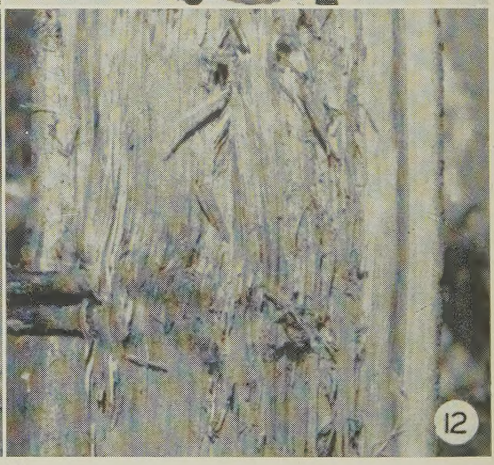


PLATE II

(*Picea sitchensis* (Bong.) Carr.) and black spruce (*P. mariana* (Mill.) B.S.P.) are either non-susceptible or only very slightly susceptible.

Reports of the occurrence of *E. tinctorium* from several distant localities led to the early conclusion that the fungus had a uniform distribution on several hosts from Alaska to Mexico and from the Pacific Ocean to the western slopes of the Rocky Mountains (28). This concept was revised by Englerth (12) who reported that the fungus does not occur west of the Cascade Mountains and by Bourchier (3) who noted its occurrence on the eastern slopes of the Rocky Mountains. More significant modifications, however, of early opinions regarding the distribution of *E. tinctorium* stem from detailed examinations of limited areas (1, 2, 6, 7, 10, 13, 26).

These studies contributed to an increasing awareness that the fungus responds in characteristic ways to different environments. In recognition of this possibility, the most recent appreciations of *E. tinctorium* were made on the premise that its distribution is related to specific environmental conditions (27, 29). These studies supported the fact of a relationship of *E. tinctorium* to specific habitats. It is now even more apparent that the fungus can no longer be evaluated effectively solely on a regional basis.

PROCEDURE

The recent accounts of *E. tinctorium* demonstrate that its distribution pattern does not fit a concept of geographical limits. It was therefore decided to assess the fungus initially on the basis of its occurrence under different conditions of forest growth. The more conventional methods of delimiting forest units were rejected for the purpose of this investigation; they were too insensitive to the frequent changes from one habitat to another. The system of classification used to provide a series of forest units within which to observe *E. tinctorium* was one that embodies the major tenets of Braun-Blanquet (4), Daubenmire (9), and Oosting (22).

The classification system used employs the plant association as its fundamental unit. It differentiates such units according to their climatic, topographic, edaphic, and floristic environments. The floristic environment of the association is defined by the occurrence, dominance, and vigor of the plants, including trees, of which it is composed. The unit of classification—the forest association—therefore is a unit of vegetation that is represented by a more or less constant floristic structure and by certain similarities in the conditions of the habitat. The area which an association occupied was designated a "site type".

PLATE II

The gross features of decay associated with *E. tinctorium*.

FIG. 7. Decay in western hemlock showing the stringy nature of its final stages and its confinement to heartwood.

FIG. 8. Decay in alpine fir is common in roots and in basal portions of stems although infections originate above the ground line.

FIG. 9. Cross-sectional views of a decay column in alpine fir at 18 ft. (lower left), 34 ft. (lower right), and 50 ft. (top) above the ground line.

FIG. 10. Decay is confined to the heartwood of stems and branches and progresses outward through the latter prior to initiation of fruiting.

FIG. 11. Decay in all stages of development in western hemlock. The mottling and dark staining of incipient decay, and the conspicuous zone lines and laminate deterioration of later stages are characteristic.

FIG. 12. Final decay in alpine fir. Decay in this stage has a stringy texture.

One advantage of such a system is that it enables recognition of specific habitats rather than an average of several. The value of previous investigations of *E. tinctorium* is limited in this regard because attempts were made to relate the variations of the fungus to one or other characteristic of a loosely defined habitat. This study employs a classification system that uses climatic, topographic, and edaphic climax types of forest vegetation as units of forest cover by which it is hoped to overcome some of the inadequacies of previous attempts to classify the conditions under which *E. tinctorium* occurs. The categories of data used to define site types and the manner of their collection were the same as reported earlier by the author (27).

British Columbia forests were examined in representative localities to learn the conditions under which *E. tinctorium* occurs and to find out if particular levels of infection could be associated with specific habitat types. The examinations were confined to stands comprised at least in part of known hosts of the fungus and which were normal stands—that is to the extent that unnatural disturbances had not occurred in them.

Most of the stands examined had reached a settled stage of maturity; for this reason they were considered to reflect the products of the operative factors of the site types they represent. Many of the site types encountered had been defined previous to this investigation and were accepted without change as suitable units of forest (19, 23, 24, 25)[4]. Some types, although previously defined, were modified for this investigation; still others were defined by the author.

Temporary plots were used both to help describe the types of habitat and for determining the frequency of *E. tinctorium* and the condition of its fruit bodies. Data were taken in such a way as to permit detection of possible influences of species of host, size and age of tree, habitat type, locality, and region. The frequency of the fungus in a given sample was interpreted in terms of the number of fruit bodies rather than in terms of total infections[5]. Such a measure of frequency, although conservative, was used because of the large amount of sampling required. It was resorted to in the knowledge that the difference between the incidence of infection and of fruiting in older stands is not great for this fungus.

An attempt was also made to evaluate the fungus according to its occurrence in the different climatic regions of British Columbia. The existence of distinct climatic regions in British Columbia results from the general northwest and southeast trend of its main structural features; they are thus at right angles to the prevailing, warm, moisture-bearing, westerly winds. This physiographic arrangement gives rise to a series of longitudinal belts of climate which, when contrasted with each other, show great differences.

After considering the fact that climatic regions of the order indicated are in themselves heterogeneous, the magnitude of the difference that exists between one region and the next appeared to justify taking such differences into account in an appraisal of *E. tinctorium*. Consequently, data pertaining to the occurrence of the fungus were related to the nine climatic regions as set forth in

[4] Additional site type information was obtained from field notes taken by Professor V. J. Krajina, Biology and Botany Department, University of British Columbia, Vancouver.

[5] The standards of frequency for fruit body occurrence were arbitrarily established in terms of the percentage of trees in a sample that bore fruit bodies, as follows: *abundant* = more than 25%, *common* = from 6 up to 25%, *infrequent* = from 2 up to 5%, *rare* = up to 2%.

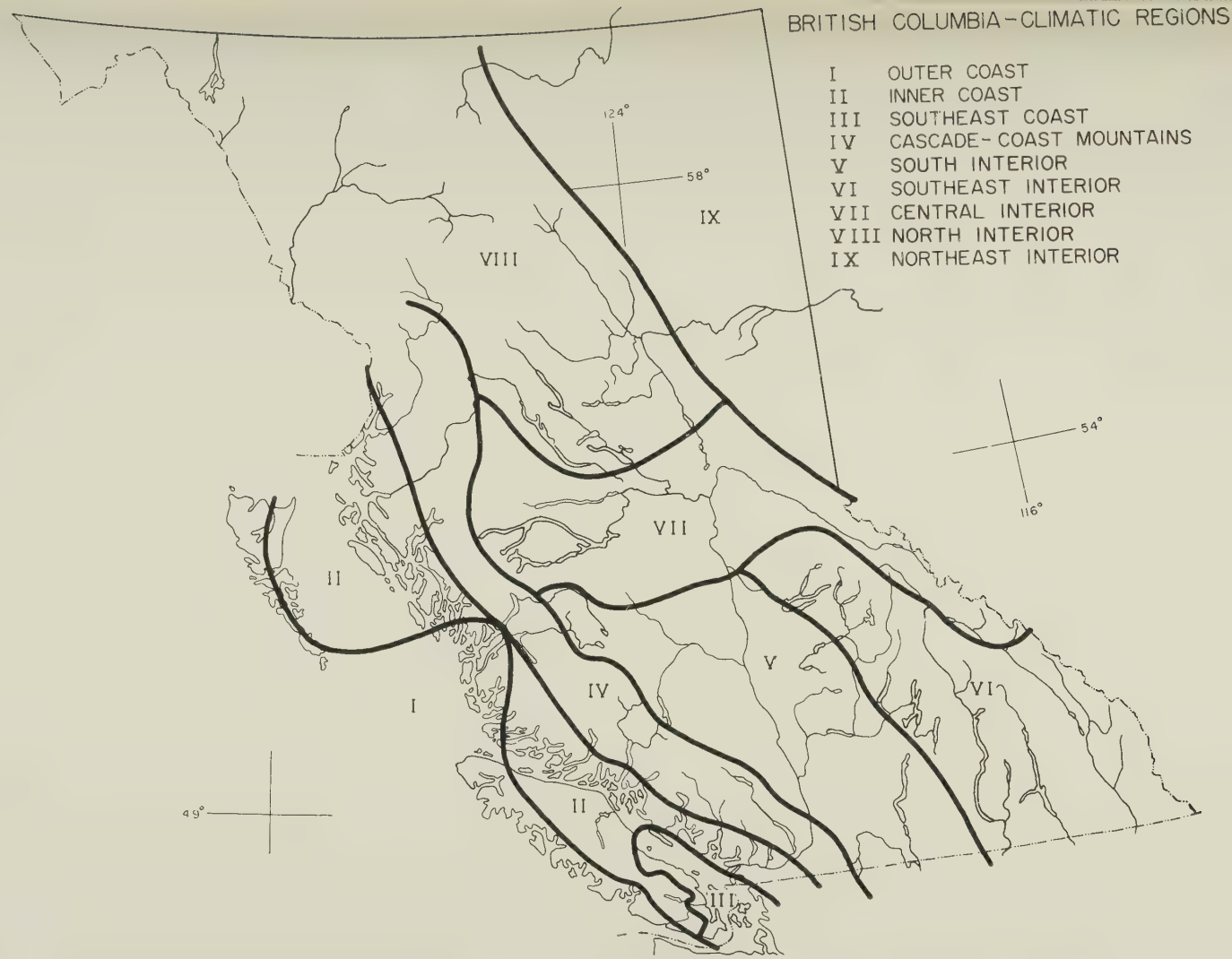


FIG. 13. The area of study. *E. tinctorium* and its hosts were classified according to their occurrence in the designated climatic regions.

Fig. 13. The regions recognized for this purpose, and the land areas encompassed by each, closely approximate those proposed by Kerr (18) and Chapman (8). The nomenclature used to describe each region follows closely that used in Resources Map 10, British Columbia Atlas of Resources (5).

THE DISTRIBUTION OF *Echinodontium tinctorium*

HABITATS

The investigation revealed a pattern of distribution for *E. tinctorium* that follows closely the occurrence of specific forest types in the Province. Thus, *E. tinctorium* was observed regularly in 34 of the 50 site types recognized. On the other hand, its absence from *all* samples of 16 site types was noted, despite the regular occurrence in them of one or more host species. A list of the habitats of *E. tinctorium* and some descriptive features of each appear in Table I.

E. tinctorium occurs in all regions of the Province with the possible exception of the southeast-coast region (Fig. 13). In terms of the number of hosts attacked and the characteristic level of infection in each, the intensity of *E. tinctorium* varies, however, from one region to another. Such inter-regional differences are sometimes great and appear to be related to major climatic features that are largely determined by air-mass movement, altitude, and latitude. Thus, apart from its apparent absence from the southeast-coast region, *E. tinctorium* has its least development in the inner-coast region and its greatest development in the southeast-interior region (Fig. 13). Yet the intensity of *E. tinctorium* varies less between regions than it does within them; little can be gained from generalizing upon the occurrence of the fungus for a whole region.

I. Outer-Coast Region—*E. tinctorium* was observed in only two of the nine host habitats of the outer-coast region, namely Habitats 5 and 6 (Table I.). The level of infection obtained in either habitat was seldom greater than *infrequent* and never exceeded *common*. The general low incidence of *E. tinctorium* that obtains for the region can be related to the regional summer climate. The mean air temperature here is about 54° F.[6] It is only in areas where summer temperatures are above average for sustained periods and where wind influences are less than normal for the region that *E. tinctorium* is found.

II. Inner-Coast Region—Forests of the inner-coast region (Fig. 13) are more uniformly and severely attacked by *E. tinctorium* than are those of the outer coast. In this region 9 of 16 habitats observed—Habitats 1 to 9 inclusive—were infected by *E. tinctorium* to various degrees up to *abundant* (Table I). The increased incidence of the fungus in inner-coast forests from that in the outer coast coincides with the warmer summer climate of the inner coast. Even in the inner-coast region, however, unless the summer temperature of an area is normally greater than the regional average (60° F.) and the total summer precipitation at least equal to the regional average (15 ins.), *E. tinctorium* does not occur. Those stands in which the fungus reached *abundant* proportions, namely in Habitats 5, 6, and 8 (Table I), were uniform to the extent of having a warm and humid aerial environment during the summer months for most of the stem length of dominant trees. Stands in which the intensity of infection by *E. tinctorium* was less than *abundant* were characterized by either drier or cooler aerial environments.

[6] Climatic values are based on data summarized by the Meteorological Division, Air Services Branch, Department of Transport (Canada). The summer period was regarded as being May to September inclusive.

TABLE I

HABITATS AND FREQUENCY OF OCCURRENCE OF *ECHINODONTIUM TINCTORIUM* IN BRITISH COLUMBIA FORESTS[1]

Prominent vegetation in habitat[2]	Climatic regions of occurrence[3]	Elevation[4]	Topography	Maximum observed frequency of *E. tinctorium*[5]
1. *Thuja plicata, Adiantum pedatum*				
Thuja plicata, Alnus oregona, Rubus parviflorus, Rubus spectabilis, Athyrium filix-femina, Adiantum pedatum, Mnium insigne, Mnium punctatum	II, IV	0–1500 (650–1100)	Alluvial benches above the flood level of rivers and streams	on *Abies amabilis* Infrequent
2. *Pinus contorta, Ledum groenlandicum, Sphagnum* spp.				
Pinus contorta, Pinus monticola, Gaultheria shallon, Ledum groenlandicum, Cornus canadensis, Vaccinium oxycoccus, Sphagnum spp.	II	0–2500 (850–1050)	Flat or gently sloping and tributary to stagnant lakes	on *Tsuga heterophylla* Infrequent
3. *Tsuga heterophylla, Gaultheria shallon*				
Pseudotsuga menziesii, Tsuga heterophylla, Gaultheria shallon, Gaultheria ovatifolia, Vaccinium ovalifolium, Vaccinium ovatifolia, Hylocomium splendens, Rhytidiopsis robusta	II	1500–3000 (1500–1950)	Upper slopes and crests of gently rolling hills or outthrusts of larger formations	on *Tsuga heterophylla* Rare
4. *Tsuga heterophylla, Abies amabilis, Blechnum spicant*				
Tsuga heterophylla, Abies amabilis, Rubus spectabilis, Blechnum spicant, Achlys triphylla, Tiarella trifoliata, Mnium insigne, Mnium punctatum	II	200–2500 (1300–2350)	Bases of slopes and well-drained but well-irrigated flat areas	on *Tsuga heterophylla* Rare *Abies amabilis* Infrequent
5. *Tsuga heterophylla, Abies amabilis, Vaccinium* spp., *Hylocomium splendens, Rhytidiadelphus loreus*				
Tsuga heterophylla, Abies amabilis, Mahonia nervosa, Vaccinium ovalifolium, Vaccinium parvifolium, Hylocomium splendens, Rhytidiadelphus loreus	I II	1000–3200 (1900–3150)	Well-drained benches or slopes	on *Tsuga heterophylla* Infrequent *Abies amabilis* Abundant

TABLE I—Continued

HABITATS AND FREQUENCY OF OCCURRENCE OF *ECHINODONTIUM TINCTORIUM* IN BRITISH OOLUMBIA FORESTS[1]—*Continued*

Prominent vegetation in habitat[2]	Climatic regions of occurrence[3]	Elevation[4]	Topography	Maximum observed frequency of *E. tinctorium*[5]
6. *Tsuga heterophylla, Thuja plicata, Gaultheria shallon*				
Tsuga heterophylla, Thuja plicata, Gaultheria shallon, Vaccinium ovalifolium, Vaccinium parvifolium, Achlys triphylla, Cornus canadensis, Hylocomium splendens	I, II	1000–3000 (1650–1800)	Steep slopes that are well-irrigated	on *Tsuga heterophylla* Rare *Abies amabilis* Abundant *Pseudotsuga menziesii* Rare
7. *Tsuga heterophylla, Chamaecyparis nootkatensis, Gaultheria shallon*				
Chamaecyparis nootkatensis, Tsuga heterophylla, Ribes sanguineum, Gaultheria shallon, Rubus pedatus, Cornus canadensis, Hylocomium splendens	II	1500–4000 (1800–3400)	Poorly drained gentle slopes or flat areas	on *Tsuga heterophylla* Infrequent *Abies amabilis* Common
8. *Tsuga heterophylla, Abies amabilis, Rubus pedatus, Rhytidiadelphus loreus, Rhytidiopsis robusta*				
Tsuga heterophylla, Abies amabilis, Vaccinium ovalifolium, Mahonia nervosa, Gaultheria ovatifolia, Rubus pedatus, Rhytidiadelphus loreus, Rhytidiopsis robusta	II	1600 3800 (1700–3700)	Benches and gentle slopes with extreme drainage and protracted snow cover	on *Tsuga heterophylla* Rare *Abies amabilis* Abundant
9. *Tsuga mertensiana, Abies amabilis, Vaccinium membranaceum*				
Tsuga mertensiana, Abies amabilis, Rhododendron albiflorum, Vaccinium membranaceum, Rubus pedatus, Viola orbiculata, Rhytidiopsis robusta, Dicranum fuscescens	II	3500–4500 (3500–3850)	Well-drained benches and slopes with protracted snow cover	on *Abies amabilis* Rare

10. *Thuja plicata, Oplopanax horridus, Dryopteris linnaeana*				
Thuja plicata, Oplopanax horridus, Cornus stolonifera, Rubus spectabilis, Dryopteris linnaeana, Tiarella unifoliata, Mnium insigne, Mnium spinulosum, Mnium punctatum	IV	1000–3500 (1100–3350)	Alluvial flood plains or at the confluence of mountain streams	on *Tsuga heterophylla* Abundant *Abies amabilis* Abundant
11. *Tsuga heterophylla, Thuja plicata, Dryopteris linnaeana*				
Tsuga heterophylla, Thuja plicata, Rubus parviflorus, Ribes lacustre, Dryopteris linnaeana, Galium triflorum, Athyrium filix-femina, Streptopus roseus	IV	700–3500 (750–3050)	Lower slopes or adjacent to but above the flood plains of mountain streams	on *Tsuga heterophylla* Common *Abies amabilis* Common
12. *Tsuga heterophylla, Abies amabilis, Vaccinium ovalifolium, Clintonia uniflora*				
Tsuga heterophylla, Abies amabilis, Vaccinium ovalifolium, Clintonia uniflora, Cornus canadensis, Tiarella unifoliata, Pyrola secunda	IV	1000–4000 (1050–3800)	Well-drained but well-irrigated slopes and benches	on *Tsuga heterophylla* Abundant *Abies amabilis* Abundant
13. *Tsuga heterophylla, Abies amabilis, Pachystima myrsinites*				
Tsuga heterophylla, Abies amabilis, Pachystima myrsinites, Linnaea borealis, Vaccinium membranaceum, Chimaphila umbellata, Calliergonella schreberi, Rhytidiopsis robusta, Hylocomium splendens	IV	1500–5000 (1500–4550)	Benches and slopes with extreme drainage	on *Tsuga heterophylla* Abundant *Tsuga mertensiana* Rare *Abies amabilis* Common *Abies lasiocarpa* Common
14. *Picea engelmannii, Abies lasiocarpa, Thalictrum occidentale*				
Picea engelmannii, Abies lasiocarpa, Menziesia ferruginea, Thalictrum occidentale, Ribes lacustre, Lonicera utahensis, Tiarella unifoliata, Valeriana sitchensis	IV V	4000–5800 (4500–5350)	Bases of slopes and alluvial benches that are former flood plains of lakes and streams	on *Abies lasiocarpa* Common

TABLE I—Continued

HABITATS AND FREQUENCY OF OCCURRENCE OF *ECHINODONTIUM TINCTORIUM* IN BRITISH COLUMBIA FORESTS[1]—*Continued*

Prominent vegetation in habitat[2]	Climatic regions of occurrence[3]	Elevation[4]	Topography	Maximum observed frequency of *E. tinctorium*[5]
15. *Picea engelmannii, Abies lasiocarpa, Vaccinium ovalifolium, Dryopteris linnaeana*				
Picea engelmannii, Abies lasiocarpa, Vaccinium ovalifolium, Vaccinium membranaceum, Menziesia ferruginea, Rubus pedatus, Dryopteris linnaeana, Streptopus roseus	IV, V	4000–5800 (4250–5300)	Bases of slopes and well-irrigated benches	on *Abies lasiocarpa* Common *Picea engelmannii*[6] Rare *Tsuga mertensiana* Infrequent
16. *Picea engelmannii, Abies lasiocarpa, Menzeisia ferruginea, Equisetum palustre*				
Picea engelmannii, Abies lasiocarpa, Menziesia ferruginea, Rhododendron albiflorum, Equisetum palustre, Equisetum pratense, Veratrum eschscholtzii, Sphagnum recurvum	V	4000–5800 (4600–5200)	Areas of restricted surface and sub-surface drainage	on *Abies lasiocarpa* Infrequent
17. *Picea engelmannii, Abies lasiocarpa, Vaccinium membranaceum*				
Picea engelmannii, Abies lasiocarpa, Rhododendron albiflorum, Vaccinium membranaceum, Pachystima myrsinites, Calliergonella schreberi, Dicranum fuscescens	IV, V, VI,	4000–5800 (4200–5600)	Crests of hills and ridges where drainage is extreme	on *Abies lasiocarpa* Common *Picea engelmannii* Rare *Tsuga heterophylla* Rare *Tsuga mertensiana* Rare
18. *Picea engelmannii, Corylus californica, Cornus stolonifera*				
Picea engelmannii, Populus trichocarpa, Corylus californica, Cornus stolonifera, Viburnum pauciflorum, Disporum oreganum, Streptopus roseus	VI	1400–3000 (2100–2900)	Recent alluvial deposits marginal to streams and lakes	on *Abies lasiocarpa* Rare *Tsuga heterophylla* Rare

19. *Thuja plicata, Tsuga heterophylla, Oplopanax horridus, Athyrium filix-femina, Dryopteris linnaeana*

Thuja plicata, Tsuga heterophylla, Oplopanax horridus, Athyrium filix-femina, Dryopteris linnaeana, Veratrum eschscholtzii, Mnium punctatum	VI, VII	1400–5000 (1550–4700)	Steep and well-irrigated slopes or marginal to streams	on *Tsuga heterophylla* Abundant *Tsuga mertensiana* Common *Abies lasiocarpa* Infrequent

20. *Thuja plicata, Athyrium filix-femina, Lysichitum americanum*

Thuja plicata, Athyrium filix-femina, Lysichitum americanum, Dryopteris linnaeana, Circaea alpina, Mnium punctatum, Brachythecium sp.	VI, VII	1400–3500 (2300–3000)	Areas that are innundated seasonally by ground water seepage	on *Tsuga heterophylla* Abundant *Abies lasiocarpa* Infrequent

21. *Tsuga heterophylla, Aralia nudicaulis, Dryopteris linnaeana, Cornus canadensis*

Tsuga heterophylla, Aralia nudicaulis, Dryopteris linnaeana, Clintonia uniflora, Tiarella unifoliata, Cornus canadensis, Maianthemum dilatatum, Ptilium crista-castrensis, Mnium punctatum	VI, VII	1400–5000 (1550–4600)	Well-irrigated slopes and benches	on *Tsuga heterophylla* Abundant *Abies grandis* Abundant *Abies lasiocarpa* Abundant *Picea engelmannii* Rare *Pseudotsuga menziesii* Rare

22. *Tsuga heterophylla, Vaccinium membranaceum, Calliergonella schreberi, Rhytidiopsis robusta*

Tsuga heterophylla, Vaccinium membranaceum, Pachystima myrsinites, Chimaphila umbellata, Linnaea borealis, Calliergonella schreberi, Rhytidiopsis robusta	VI, VII	1400–5000 (1450–4450)	Well-drained slopes and benches	on *Tsuga heterophylla* Abundant *Abies grandis* Abundant *Abies lasiocarpa* Common

23. *Pseudotsuga menziesii, Arctostaphylos uva-ursi, Dicranum scoparium*

Pseudotsuga menziesii, Pinus monticola, Vaccinium membranaceum, Pachystima myrsinites, Arctostaphylos uva-ursi, Apocynum androsaemifolium, Dicranum scoparium	VI	1400–4500 (1450–4350)	Areas having extreme drainage	on *Tsuga heterophylla* Common

TABLE I—Continued

HABITATS AND FREQUENCY OF OCCURRENCE OF *ECHINODONTIUM TINCTORIUM* IN BRITISH COLUMBIA FORESTS[1]—*Concluded*

Prominent vegetation in habitat[2]	Climatic regions of occurrence[3]	Elevation[4]	Topography	Maximum observed frequency of *E. tinctorium*[5]
24. *Abies lasiocarpa, Vaccinium membranaceum, Calliergonella schreberi*				
Abies lasiocarpa, Menziesia ferruginea, Vaccinium membranaceum, Rubus pedatus, Linnaea borealis, Callieryonella schreberi, Rhytidiadelphus triquetrus	VI, VII	2000–5500 (3050–5000)	Well-drained slopes and benches in areas with protracted snow cover	on *Abies lasiocarpa* Abundant *Tsuga heterophylla* Common *Tsuga mertensiana* Abundant
25. *Picea sitchensis, Cornus stolonifera, Athyrium filix-femina*				
Picea sitchensis, Populus trichocarpa, Cornus stolonifera, Sambucus melanocarpa, Oplopanax horridus, Athyrium filix-femina, Dryopteris linnaeana	IV	0–400 (150–350)	Flood plains of rivers and lakes	on *Tsuga heterophylla* Common *Abies amabilis* Infrequent
26. *Thuja plicata, Tsuga heterophylla, Oplopanax horridus, Rubus spectabilis*				
Thuja plicata, Tsuga heterophylla, Oplopanax horridus, Athyrium filix-femina, Rubus spectabilis, Pteritis nodulosa, Mnium insigne	IV	0–700 (150–400)	Bases of slopes and alluvial benches	on *Tsuga heterophylla* Infrequent *Abies amabilis* Common
27. *Tsuga heterophylla, Abies amabilis, Dryopteris linnaeana, Dryopteris dilatata*				
Tsuga heterophylla, Abies amabilis, Rubus parviflorus, Dryopteris dilatata, Dryopteris linnaeana, Tiarella unifoliata, Rhytidiadelphus loreus	IV	300–3000 (650–1200)	Well-irrigated and well-drained slopes and benches	on *Tsuga heterophylla* Common *Abies amabilis* Common

28. *Tsuga heterophylla, Abies amabilis, Vaccinium ovalifolium, Hylocomium splendens*

Tsuga heterophylla, Abies amabilis, Vaccinium ovalifolium, Clintonia uniflora, Cornus canadensis, Hylocomium splendens, Rhytidiadelphus loreus	IV	300–3000 (950–2900)	Well-drained slopes and benches lacking sub-surface irrigation	on *Tsuga heterophylla* Common *Abies amabilis* Abundant

29. *Tsuga heterophylla, Menziesia ferruginea, Hylocomium splendens, Calliergonella schreberi*

Tsuga heterophylla, Pinus contorta, Menziesia ferruginea, Vaccinium ovalifolium, Chimaphila umbellata, Hylocomium splendens, Calliergonella schreberi	IV	250–1500 (600–950)	Areas having extreme drainage	on *Tsuga heterophylla* Common *Abies amabilis* Infrequent

30. *Picea glauca* var. *albertiana, Lonicera involucrata, Athyrium filix-femina*

Picea glauca var. *albertiana, Alnus tenuifolia, Lonicera involucrata, Athyrium filix-femina, Dryopteris linnaeana, Dryopteris dilatata*	VII, VIII	2000–2200 (2000–2150)	Flood plains of streams and lakes	on *Abies lasiocarpa* Infrequent *Picea glauca* var. *albertiana*$_6$ Rare

31. *Picea glauca* var. *albertiana, Abies lasiocarpa, Oplopanax horridus*

Picea glauca var. *albertiana, Abies lasiocarpa, Oplopanax horridus, Viburnum pauciflorum, Athyrium filix-femina, Mnium punctatum*	VII, VIII	2000–3200 (2100–2450)	Gentle slopes or bases of steep slopes having a permanently high water table	on *Tsuga heterophylla* Infrequent *Picea glauca* var. *albertiana*$_6$ Rare *Abies lasiocarpa* Common

32. *Picea glauca* var. *albertiana, Abies lasiocarpa, Rubus parviflorus, Disporum oreganum*

Picea glauca var. *albertiana, Abies lasiocarpa, Rubus parviflorus, Disporum oreganum, Streptopus roseus, Petasites speciosa*	VII, VIII	2000 3500 (2000–2700)	Well-drained slopes that are seasonally deficient in ground water	on *Abies lasiocarpa* Infrequent *Picea glauca* var. *albertiana*$_6$ Rare

TABLE I—Concluded

HABITATS AND FREQUENCY OF OCCURRENCE OF *ECHINODONTIUM TINCTORIUM* IN BRITISH COLUMBIA FORESTS[1]—*Concluded*

Prominent vegetation in habitat[2]	Climatic regions of occurrence[3]	Elevation[4]	Topography	Maximum observed frequency of *E. tinctorium*[5]
33. *Picea glauca* var. *albertiana, Abies lasiocarpa, Aralia nudicaulis, Dryopteris linnaeana*				
Picea glauca var. *albertiana, Abies lasiocarpa, Aralia nudicaulis, Dryopteris linnaeana, Ptilium crista-castrensis, Rhytidiadelphus triquetrus*	VII, VIII	2000-3500 (2000–2750)	Well-drained and well-irrigated slopes and benches	on *Abies lasiocarpa* Common *Tsuga heterophylla* Infrequent *Picea glauca* var. *albertiana*[6] Rare
34. *Picea glauca* var. *albertiana, Abies lasiocarpa, Equisetum sylvaticum, Sphagnum recurvum*				
Picea glauca var. *albertiana, Abies lasiocarpa, Ledum groenlandicum, Equisetum sylvaticum, Sphagnum recurvum, Calliergonella schreberi*	VII, VIII	2000–3200 (2100–2650)	Flat areas with restricted sub-surface drainage	on *Abies lasiocarpa* Common *Tsuga heterophylla* Infrequent *Picea glauca* var. *albertiana*[6] Rare

[1] Based on 493 sample plots.

[2] The nomenclature used for trees is that given by Can. Dept. Mines and Res. For. Serv. Bull. 61, 5th ed., "Native trees of Canada", and for subordinate vegetation as given by M. E. Peck, "A manual of the higher plants of Oregon", J. K. Henry, "Flora of southern British Columbia", and H. S. Conard, "How to know the mosses".

[3] Climatic regions are as follows: I = outer-coast, II = inner-coast, III = southeast-coast, IV = Cascade-Coast Mountains, V = south-interior, VI = southeast-interior, VII = central-interior, VIII = north-interior, IX = northeast-interior.

[4] The observed altitudinal limits of habitats and (in brackets) of *E. tinctorium*.

[5] Expressed as the percentage of sporophore-bearing trees in the sample, namely, *abundant* = more than 25 per cent, *common* = from 6 to 25 per cent, *infrequent* = from 2 to 5 per cent, *rare* = up to 2 per cent.

[6] *E. tinctorium* confirmed on the basis of its isolation from decayed wood.

III. Southeast-Coast Region—No evidence of *E. tinctorium* was observed in this region despite the presence of host trees.

IV. Cascade-Coast Mountains Region—The forests here are similar to those of the inner-coast region as regards a diversity of host habitats but differ widely in the degree to which they are attacked by *E. tinctorium.* Thirteen of the 16 habitats of this region are infected to various degrees, namely Habitats 1, 10 to 15, 17, and 25 to 29 (Table I). *E. tinctorium* reaches *abundant* proportions in four of these, namely Habitats 10, 12, 13, 28, and is at least *common* in several others. The region features a great altitudinal range and a similar range of summer climates. In general, however, the summer climate is warmer than that of the inner-coast region. *E. tinctorium* becomes less frequent in the Cascade-Coast Mountain region with increasing altitude, coincident with a regional trend of increasing dryness with increasing altitude. Many of the sub-alpine stands of the region have a very dry summer climate and a low incidence of infection. The dryness of such stands is conditioned by low summer precipitation and is accentuated by regular drying winds; these are less frequent at lower elevations and here *E. tinctorium* is more abundant.

V. South-Interior Region—Only 4 of 11 host habitats observed for the south-interior region (Fig. 13) contained *E. tinctorium,* all of which are sub-alpine, namely Habitats 14 to 17 (Table I). The maximum frequency of *E. tinctorium* observed for the region was *common* and, in general, the intensity of infection was less. The region features an even greater range of summer climates than does the Cascade-Coast Mountains region because of its generally lower precipitation and higher temperature. Temperatures decrease and precipitation increases with increasing altitude in the south interior. The climate favors the occurrence of *E. tinctorium* only at elevations greater than 3,000 feet. Even at elevations where the climate permits the fungus to occur, the requisite conditions of temperature and moisture seldom obtain much above the height of the lower half of dominant trees. Above this height the atmosphere within stands is very dry during summer months, largely the result of drying winds.

VI. Southeast-Interior Region—This more than any other region of the Province is uniformly and seriously affected by *E. tinctorium.* The fungus occurs in 8 of its 9 host habitats, namely Habitats 17 to 24 (Table I), and reaches *abundant* proportions in five, Habitats 19 to 22, and 24. The regional summer climate, which has a mean temperature of about 63° F. and a precipitation of from 4 to 12 inches, generally favors the development of *E. tinctorium.* But the fungus was not observed in areas where the low extremes of either temperature or precipitation prevail. Unlike the Cascade-Coast Mountains region the intensity of infection remains high in high-elevation forests of the southeast interior, up to approximately 5,000 feet.

VII. Central-Interior Region—This region lacks the physiographic variety of most of the other regions of the Province. Consequently, it has a fairly uniform summer climate which, although cooler than that of the southeast interior, has about the same precipitation, approximately 9 inches. *E. tinctorium* has a uniform distribution in the region, occurring in all 10 of its host habitats, namely Habitats 19 to 22, 24, 30 to 34 (Table I). The intensity of infection is seldom greater than *common* except in two habitats, namely Habitats 21 and 22 (Table I), where it reaches *abundant* proportions.

Regions VIII and IX—The north-interior and northeast-interior regions (Regions VIII and IX, Fig. 13), although examined in less detail than other regions of the Province, appear to have a general low incidence of *E. tinctorium.* On the basis of a limited examination it would appear that the summer climates of both regions are too cool, and occasionally too dry, to admit *E. tinctorium* in high frequencies.

Hosts

The investigation left the list of known hosts of *E. tinctorium* unchanged for British Columbia from that revealed by previous investigations: alpine fir, amabilis fir, Douglas fir, grand fir, mountain hemlock, western hemlock, Engelmann spruce, and western white spruce. This study confirms that the species listed are susceptible and showed that some are more susceptible to infection by *E. tinctorium* than others. Further, the investigation showed that each species of host is severely attacked in only some of its natural habitats. An appreciation of the degree to which *E. tinctorium* infects its different hosts in British Columbia is presented in Table II.

No species is infected in all of its natural habitats, and seldom are all host species of a habitat infected. It would appear from this that the occurrence of a host species is in itself no criterion of its being infected by *E. tinctorium.* In fact, the investigation showed that the circumstances under which individual trees occur in a stand—their dominance position, vigor, pruning habit, and age—are more reliable criteria of infection. The silvicultural characteristics of a host species are similar in stands of a particular site type and differ from one site type to another. Infection by *E. tinctorium* can be related to the condition of its hosts. Thus, it is possible to predict characteristic levels of infection not only for individual habitats but also for each host species in each of its natural habitats.

Alpine fir—This tree is attacked regularly by *E. tinctorium* in all but one of the 17 habitats observed for this species of host, namely Habitat 23 (Table I). Although infected with great regularity throughout its range, the intensity of infection on alpine fir is *abundant* in only two habitats, namely Habitats 13 and 24 (Table I), and nowhere exceeded 30 per cent of the trees in individual stands. Alpine fir occurs in all canopies in all of its habitats and is attacked by *E. tinctorium* quite uniformly in each (Table II).

Such a uniform pattern of infection appears to result from the fact that conditions most favorable to infection by *E. tinctorium* (sustained high humidities and air temperatures during summer months) occur in a stratum below the midpoint of dominant trees in alpine fir stands. Thus, all trees of such stands are exposed to infection. The fact that many alpine firs are not infected appears to result from a specific degree of natural resistance to infection.

Amabilis fir—This species is attacked by *E. tinctorium* in at least 16 of the 24 habitat types of which it is a regular component (Table II). The intensity of infection reaches *abundant* proportions on this species in six habitats, namely Habitats 5, 6, 8, 10, 12, 28 (Table I), and is at least *common* in several others. Unlike alpine fir, amabilis fir is much more heavily attacked at heights above the midpoint of dominant trees. Consequently, trees of intermediate height, and less, often escape infection by *E. tinctorium* (Table II). This scarcity of infection in low-canopy trees can be accounted for by the cool atmosphere that occurs close to the ground in most stands of amabilis fir. Some amabilis fir habitats admit

TABLE II

OCCURRENCE OF *ECHINODONTIUM TINCTORIUM* AND ITS HOSTS IN BRITISH COLUMBIA FORESTS[1]

Tree layer[2]	Number of habitats in which					
	Host occurs	Fungus occurs	Maximum frequency[3] of the fungus is			
			Abundant	Common	Infrequent	Rare
			Abies lasiocarpa			
A 1	17	15	2	5	4	4
A 2	17	16	2	4	5	5
B 1	17	15	.....	7	6	2
A or B	17	16	2	8	4	2
			Abies amabilis			
A 1	16	15	6	5	2	2
A 2	20	14	.....	8	4	2
B 1	24	13	.....	4	6	3
A or B	24	16	6	5	3	2
			Pseudotsuga menziesii			
A 1	35	2	.....	.....	.....	2
A 2	23	.....	.....	.....	.....	.....
B 1	14	.....	.....	.....	.....	.....
A or B	35	2	.....	.....	.....	2
			Abies grandis			
A 1	7	2	2	.....	.....	.....
A 2	6	2	2	.....	.....	.....
B 1	6	2	.....	1	1	.....
A or B	8	2	2	.....	.....	.....
			Tsuga mertensiana			
A 1	6	2	1	.....	.....	1
A 2	8	1	.....	1	.....	.....
B 1	12	4	.....	.....	2	2
A or B	12	5	1	.....	1	3
			Tsuga heterophylla			
A 1	29	22	7	5	5	5
A 2	36	20	6	5	3	6
B 1	42	19	3	7	2	7
A or B	42	27	7	5	5	10
			Picea engelmannii			
A 1	14	1	.....	.....	.....	1
A 2	13	.....	.....	.....	.....	.....
B 1	12	.....	.....	.....	.....	.....
A or B	14	1	.....	.....	.....	1
			Picea glauca var. *albertiana*			
A 1	5	.....	.....	.....	.....	.....
A 2	5	.....	.....	.....	.....	.....
B 1	5	.....	.....	.....	.....	.....
A or B	5	.....	.....	.....	.....	.....
			All hosts			
A 1	49	33	12	10	5	6
A 2	49	32	6	13	7	6
B 1	50	28	3	14	9	2
A or B	50	34	12	13	6	3

[1] Data based on 493 examinations of 50 habitat types.

[2] *A 1* = dominant and codominant trees, *A 2* = intermediate trees, *B 1* = overtopped trees more than 6 feet in height,

[3] Expressed as the percentage of sporophore-bearing trees in the sample, namely, *Abundant* = more than 25 per cent. *Common* = from 6 up to 25 per cent, *Infrequent* = from 2 up to 5 per cent, *Rare* = up to 2 per cent.

this host tree only into the lower canopies with the result that amabilis fir is not infected by *E. tinctorium* while other host species that reach into higher canopies are infected. Hence, amabilis fir escapes infection in eight of its natural habitats.

Douglas fir—This tree is seldom attacked by *E. tinctorium* but is infected in two habitats at least, namely Habitats 6 and 21 (Table I). Despite a general high incidence of infection on its co-species—mainly amabilis fir, grand fir, alpine fir, and western hemlock—the maximum infection recorded for Douglas fir was *rare*.

Grand fir—This species is free from attack by *E. tinctorium* in its six coastal habitats but is infected in *abundant* proportions in its two interior habitats, Habitats 21 and 22 (Table I). The absence of *E. tinctorium* from grand fir in coastal forests may be accounted for by the cool summer climate found in its coastal habitats. On the other hand, the summer climate of the interior habitats where *E. tinctorium* is *abundant* on grand fir is warm and humid for most of the summer.

Mountain hemlock—Infection is found in at least five of its natural habitats, 13, 15, 16, 19, 24 (Table I). The intensity of infection on this species of host varies from one habitat to another but reaches *abundant* proportions in at least one, Habitat 24. *E. tinctorium* was not observed on mountain hemlock in coastal forests and reaches its maximum development on this species in the southeast-interior region (Fig. 13).

Western hemlock—The fungus attacks trees in 27 of the 42 habitats observed for the species. The intensity of infection reaches *abundant* proportions in at least seven habitats, 10, 12, 13, and 19 to 22 (Table I). *E. tinctorium* occurs on western hemlock in all regions of the Province but has a consistently low frequency in coastal forests, where infections are mostly confined to the upper half of dominant trees. Understory western hemlocks are seldom infected in coastal forests.

Western hemlock is infected to a much greater extent in the Cascade and Coast Mountains than in coastal forests. There is a much higher incidence of the fungus in low-canopy trees as well as a higher incidence in upper-canopy trees. Similarly, and even to a greater extent, the pattern of infection on western hemlock is uniformly *abundant* in all canopies of many stands in the southeast-interior region (Fig. 13).

The atmospheric environments of stands having an *abundant* occurrence of *E. tinctorium* on western hemlock are similar throughout the Province; high temperatures and humidities prevail from close to the ground to the tops of trees during summer months. Any departure from such an atmospheric condition in western hemlock stands is accompanied by a reduced occurrence of *E. tinctorium* on this species.

Engelmann spruce—The intensity of infection by *E. tinctorium* on Engelmann spruce is invariably low in the three habitats in which the fungus has been observed on this species of host, Habitats 15, 16, 21 (Table I). *E. tinctorium* seldom fruits on Engelmann spruce and the incidence of the fungus remains low even in stands where its co-species—mainly alpine fir, amabilis fir, and western hemlock—are heavily infected and bear fruit bodies regularly.

Western white spruce—On the basis of its isolation from decayed wood, *E. tinctorium* attacks western white spruce in five habitats, namely Habitats 30 to 34 (Table I), all of which occur in central and northern British Columbia (Fig. 13). *E. tinctorium* does not appear to fruit on this host. The intensity of infection on western white spruce is invariably *rare* in all its habitats despite a much higher incidence on its major co-species, alpine fir.

OBSERVATIONS ON THE ECOLOGY OF THE DISTRIBUTION OF *Echinodontium tinctorium*

The reasons for the presence or absence of *E. tinctorium* in particular stands are seemingly numerous and interacting, but the pattern of distribution for the fungus appears to be closely identified with climate. The yearly climate of a locality may influence *E. tinctorium*, but its summer climate is particularly important; the external development of the fungus occurs during that period. Significantly, the abundance of *E. tinctorium* increases from west to east and north to south in British Columbia. This coincides with increasing summer temperatures along the same general axes. Equally significant, however, is the fact that a high average summer temperature does not itself guarantee the occurrence of *E. tinctorium*. However, high average summer temperatures combined with sustained high humidities do provide a reliable criterion of the presence of *E. tinctorium*.

There appears to be no set pattern of circumstances that provides the requisite climatic condition for development of *E. tinctorium*. Such conditions are made possible by a wide range of conditions such as: normally high summer temperatures; a low degree of shading within stands; restricted air drainage or protection from persistent winds; frequent summer rains; evaporation from surface accumulations of water; delayed surface and sub-surface runoff; and transpiration from a luxuriant lower vegetation. Whatever the combination of favorable environmental circumstances it must include a summer climate that features a high average summer temperature and high humidities if *E. tinctorium* is to develop.

The duration of favorable atmospheric conditions and the proportion of the stem length of trees over which they prevail will largely determine the abundance of *E. tinctorium* in individual stands. If a suitable atmosphere is of short duration and prevails over a limited proportion of the stem length of susceptible trees the intensity of infection by *E. tinctorium* is correspondingly low. This condition applies generally in coastal forests where *E. tinctorium* occurs sporadically, mainly high above the ground. On the other hand, if a suitable atmosphere is of extended duration and prevails over a major portion of the stem length of trees, infections are frequent and take place over an extensive portion of individual tree stems. This condition applies to stands of Cascade-Mountain and southeast-interior forests.

It is recognized that the requirement of a suitable atmosphere for *E. tinctorium* and the duration and location of this condition influence the abundance of the fungus. From this, it is evident that the growth characteristics of individual trees and trees of different species can influence their susceptibility to infection. Species having a low frequency in the dominant canopy of stands are seldom infected when conditions favorable to infection occur only high above

ground. Hence, for example, amabilis fir escapes infection in Habitat 3 and is attacked in Habitat 13 to a lower degree than is western hemlock (Table I).

Apart from climate, a major factor in the distribution of *E. tinctorium* is the inherent susceptibility to infection by some tree species. The vulnerability to infection by *E. tinctorium* varies greatly among its different hosts. Part of this variation is clearly the result of the characteristics of the environments within which the different species of host are most commonly found. Yet, repeated examples of a co-occurrence of hosts are found where one shows more infection than the other.

Western hemlock and amabilis fir occur together as dominant trees in at least 14 habitat types, all of which admit *E. tinctorium* on both hosts of this class. The intensity of infection on amabilis fir, however, exceeds that on western hemlock in seven habitat types and equals it in the remaining seven. Similarly, *E. tinctorium* occurs on dominant alpine firs in 11 of 12 habitat types in which Engelmann spruce also occurs in the dominant canopy. Engelmann spruce, however, is infected in only three habitat types and to a much lower degree than alpine fir. On the basis of the current investigation it would appear that *Abies* spp. are more subject to attack by *E. tinctorium* than are *Tsuga* spp., *Picea* spp., and *Pseudotsuga menziesii*. Furthermore, *P. menziesii* and *Picea* spp. appear to be attacked only occasionally and seldom, if ever, to the degree that other hosts are attacked.

The occurrence and abundance of *E. tinctorium* is influenced indirectly by a number of factors among which are altitude, topography, and vigor of the host trees. The fact that *E. tinctorium* does not have a uniform distribution within prescribed altitudinal limits in any locality or region would indicate that altitude does not act independently of other factors to control the distribution of the fungus. But altitude does have a profound effect upon *E. tinctorium* because it helps determine the nature of regional and sub-regional climates. Similarly, topography can have a great influence upon the presence and abundance of *E. tinctorium*. It is not a single or independent factor but acts together with other factors, such as altitude.

Altitude can determine the nature of sub-regional climates and hence the general distribution of *E. tinctorium* in a region; topography will to a large degree determine the nature of local climates and hence the distribution of *E. tinctorium* in a particular locality or stand. Thus, sub-alpine forests of the south-interior region have a climate that generally favors an abundance of *E. tinctorium*, largely because of their elevation above the dry valleys of the region. Because of local topography, however, the climate of these forests is in fact a composite of local climates. Consequently, there occurs a mosaic of habitat types each with its specific level of infection by *E. tinctorium*. Similar examples of sub-regional and local climatic variations are found in all regions of the Province with the result that each region contains a multiplicity of habitat types. Individual habitat types do not, however, conform to narrow altitudinal limits or to a specific topography.

Vigor of host trees appears to influence susceptibility to infection by *E. tinctorium*. Reduced vigor in all its hosts, whether caused by suppression through over-topping or resulting from a natural inability to flourish in a particular

habitat, is usually accompanied by increased infection by *E. tinctorium.* Maximum intensities of infection are invariably associated with greatly reduced vigor of hosts, although not usually with their least vigorous condition.

The coincidence of low vigor of its hosts with increased infection by *E. tinctorium* appears to result from the pruning habit of non-vigorous trees; they retain dead branches and branch stubs longer than vigorous trees. This characteristic of non-vigorous trees, in light of the fact that most infections originate in branch stubs, is of great importance in relation to the abundance of *E. tinctorium.* Most of the hosts of *E. tinctorium* that are infected in *abundant* proportions—alpine fir, amabilis fir, mountain hemlock, and western hemlock—are shade-tolerant species. Even on good sites such species frequently undergo a sustained period of low vigor during which natural pruning is very inefficient. On the other hand, species that are relatively intolerant to shade—grand fir in coastal forests, Douglas fir, Engelmann spruce, and western white spruce—are less likely to undergo sustained periods of low vigor than are shade-tolerant species. Such species are not seriously affected by *E. tinctorium.*

The many isolated occurrences of *E. tinctorium* that characterize its distribution in British Columbia can be shown to coincide with isolated occurrences of habitats which are more extensive in other areas. Hence, there appears to be little foundation in the premise that *E. tinctorium* has an unusually broad ecological tolerance. On the contrary, it can be demonstrated that *E. tinctorium* has an ecological tolerance less broad than that of any of its hosts.

SUMMARY

A survey involving the examination of known hosts of *E. tinctorium* showed that the fungus occurs on at least one of its hosts in all regions of the Province except the southeast-coast region (Fig. 13). On the basis of the number of host species attacked and the intensity of infection on each, *E. tinctorium* is least abundant in the outer-coast region and is most abundant in the southeast-interior region. Inter-regional differences in the abundance of the fungus of the order indicated appear to be related to major climatic features that are largely determined by air-mass movement, altitude, and latitude. Hence, the fungus demonstrates a pattern of increasing abundance from west to east and north to south.

Although there are recognizable differences in the abundance of *E. tinctorium* between regions, more pronounced differences occur within regions. Thus, the distribution and abundance of the fungus closely follows the occurrence of specific forest types, some of which admit the fungus in characteristic frequencies and others which exclude it. Thirty-four forest types of the total of 50 recognized for purposes of the investigation showed some infection; but the fungus was absent from 16 forest types despite the occurrence in them of one or more of its known hosts (Table II).

The distribution and abundance of *E. tinctorium* appear to be influenced directly, (1) by the nature of the summer climate of particular areas and (2) by the inherent susceptibilities to infection of its different hosts. Factors that influence the fungus indirectly include altitude, topography, and the silvical characteristics of individual trees and trees of different species.

It is evident that high average summer temperatures in combination with sustained high humidities provide a reliable criterion of the presence of *E. tinctorium* in particular areas. On the other hand, the abundance of the fungus in individual stands is largely determined by the proportion of the stem length of trees over which favorable atmospheric conditions prevail. Hence in south-coast forests, where infections are generally few in number, the requisite conditions for infections to take place are characteristically confined to the upper portions of trees. Forests of the southeast interior and the Cascade Mountains are often abundantly infected, largely because the requisite conditions of temperature and moisture generally occur over the full length of the tree stems. Similarly, the duration of favorable atmospheric conditions can influence the level of infection that is possible for particular stands.

None of the eight known hosts of *E. tinctorium* are attacked in all of their natural habitats, although some hosts are attacked more frequently than others (Table II). On the basis of the co-occurrence of hosts of different species, whereby some are infected and others remain free from infection, it would appear that degrees of susceptibility to infection by *E. tinctorium* exist among its different hosts. Thus, *Abies* spp. appear to be more subject to attack than are *Tsuga* spp., *Picea* spp., and *Pseudotsuga menziesii*.

Although *E. tinctorium* does not have a uniform distribution within prescribed altitudinal limits in any locality or region, altitude has a profound effect upon the fungus because of its role in determining the nature of regional and subregional climates. On the other hand, topography determines to a large degree the nature of climates within individual stands of a region and, therefore, the distribution in them of *E. tinctorium*.

The growth habits of individual trees and trees of different species play important roles in determining the level of infection by *E. tinctorium*. Hence maximum intensities of infection are invariably associated with greatly reduced vigor of hosts, although not usually with their least vigorous condition. In this regard the pruning habit of non-vigorous trees, which is to retain dead branches longer than vigorous trees, is of considerable importance in relation to the abundance of *E. tinctorium* because most infections originate in branch stubs. The heights that individual trees and trees of different species attain in specific sites is sometimes a factor in the possibility of infection by *E. tinctorium*. Thus, trees that do not occupy the highest canopy level are seldom infected when the conditions for infection occur only high above the ground. It is largely by such means that amabilis fir escapes infection in 8 of its 24 natural habitats.

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